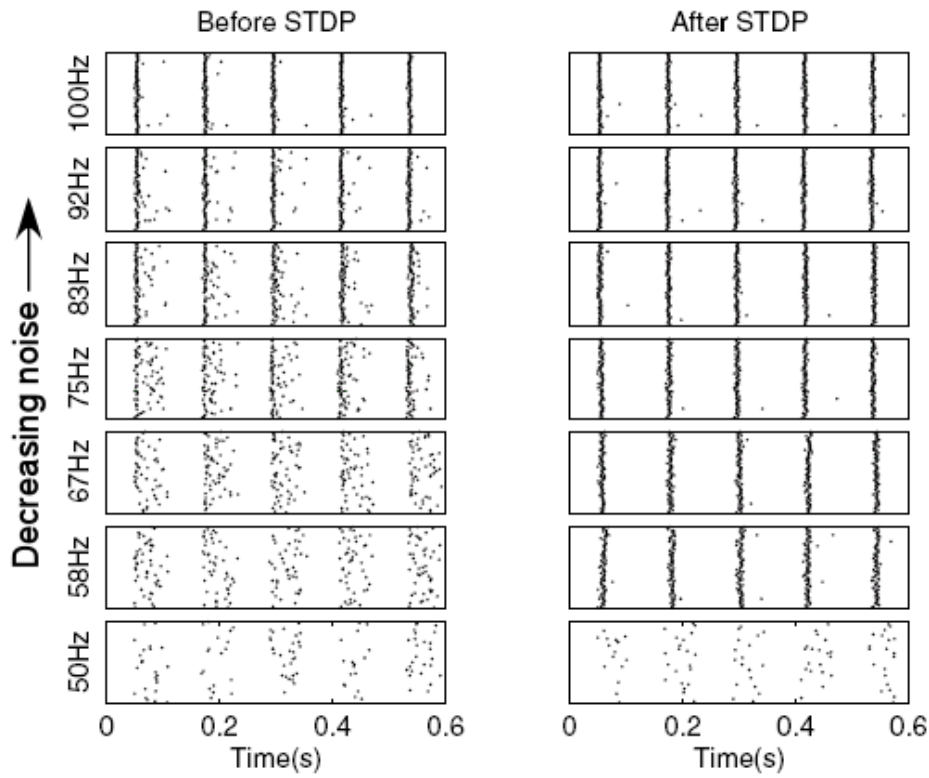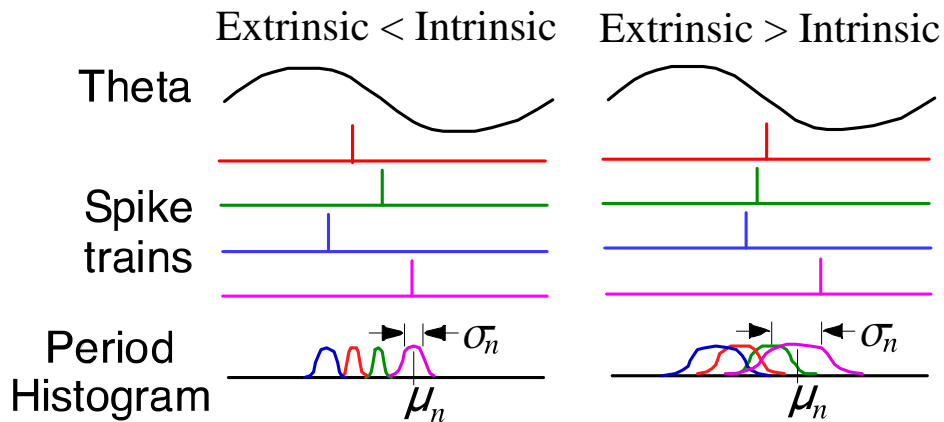# Limits of STDP



STDP fails to improve phase-coding when input is too noisy (50Hz Poisson input).

**Two hypotheses for why STDP fails with noisy inputs:**
   **1. Both pre-post and post-pre pairings start occuring.**
   **2. Pairings fall outside the STDP window.**

# Two sources of timing variability



Neuron $n$ spikes at times distributed with mean $\mu_n$ and sigma $\sigma_n$, as dictated by intrinsic and extrinsic variability, respectively.

These sources of variability are computed from the spike-times $t_{nm}$ of $n = 1 \ldots N$ neurons recorded over $m = 1 \ldots M$ cycles as follows.

*Notation*: $\langle t_n \rangle_m$ is the mean phase of neuron $n$'s spike, computed over M trials, while $\langle t \rangle_{nm}$ is mean phase of all the neurons, computed over all the trials.

**Intrinsic:** Due to differences in excitability among neurons, which determine the distribution of spike times in the absence of noise. We quantify this source as the variance of the means:

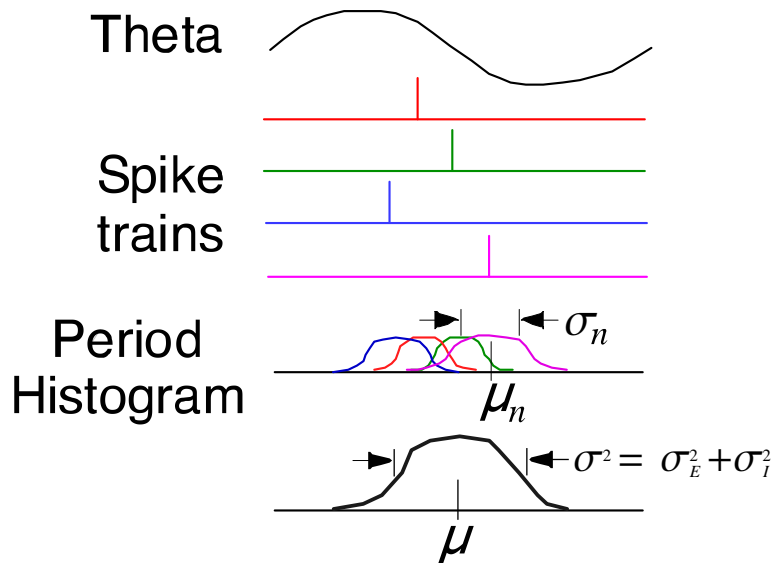$$\sigma_I^2 = \sigma^2[\mu_n] = \frac{1}{N} \sum_{n=1}^{N} (\langle t_n \rangle_m - \langle t \rangle_{nm})^2$$

**Extrinsic**: Due to noise in the neurons' inputs, which determines the jitter in individual neuron's spikes. We quantify this source as the mean of the variances:

$$\sigma_E^2 = \mu[\sigma_n^2] = \frac{1}{N} \sum_{n=1}^{N} \frac{1}{M} \sum_{m=1}^{M} (t_{nm} - \langle t_n \rangle_m)^2$$

When $\sigma_E > \sigma_I$, the order of spikes changes from cycle to cycle.

# These two sources' variances add



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Spike times' variance, $\sigma^2$, is the sum of extrinsic and intrinsic variances, $\sigma_E^2$ and $\sigma_I^2$.

The variance of spike-times of $n = 1 \ldots N$ neurons over $m = 1 \ldots M$ cycles is given by:

$$\sigma^2 = \frac{1}{N\,M} \sum_{m=1}^{M} \sum_{n=1}^{N} (t_{nm} - \langle t \rangle_{nm})^2$$

$$= \frac{1}{N\,M} \sum_{m=1}^{M} \sum_{n=1}^{N} (t_{nm} - \langle t_n \rangle_m + \langle t_n \rangle_m - \langle t \rangle_{nm})^2$$

$$= \frac{1}{N\,M} \sum_{m=1}^{M} \sum_{n=1}^{N} (t_{nm} - \langle t_n \rangle_m)^2 + (\langle t_n \rangle_m - \langle t \rangle_{nm})^2$$

$$\qquad + (t_{nm} - \langle t_n \rangle_m)\ (\langle t_n \rangle_m - \langle t \rangle_{nm})$$

$$= \frac{1}{N} \sum_{n=1}^{N} \frac{1}{M} \sum_{m=1}^{M} (t_{nm} - \langle t_n \rangle_m)^2 + \frac{1}{N} \sum_{n=1}^{N} (\langle t_n \rangle_m - \langle t \rangle_{nm})^2$$
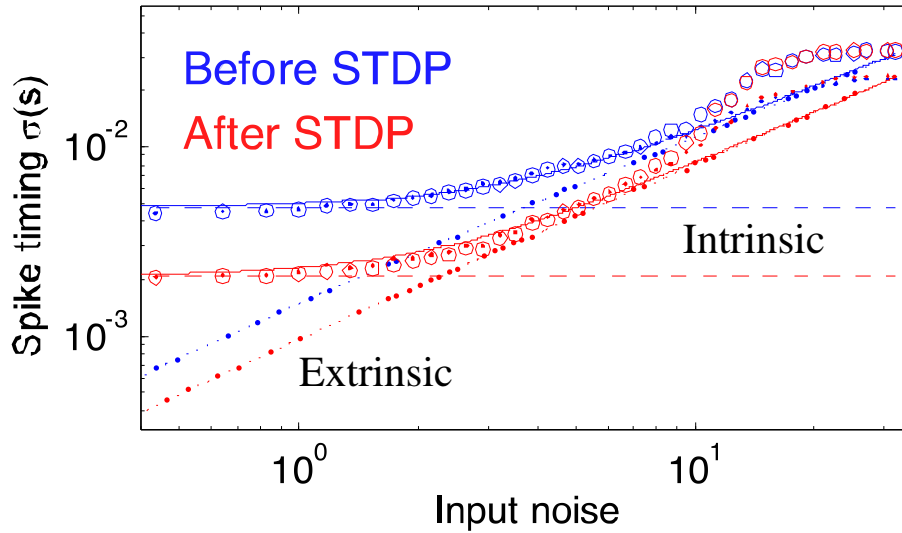
$$= \sigma_E{}^2 + \sigma_I{}^2$$

where

$$\sigma_I{}^2 = \sigma^2[\mu_n] \quad \text{and} \quad \sigma_E{}^2 = \mu[\sigma_n{}^2]$$

are the extrinsic and intrinsic components of timing-precision.

The intuition here is that the actual spike phase can be obtained by summing two random variables, drawn from distributions that describe the mean time the neuron fires (intrinsic variability) and the jitter around that mean (extrinsic variability). Hence, $\sigma^2(X+Y)=\sigma^2(X)+\sigma^2(Y)$, where X corresponds to mean and Y correspond to jitter.
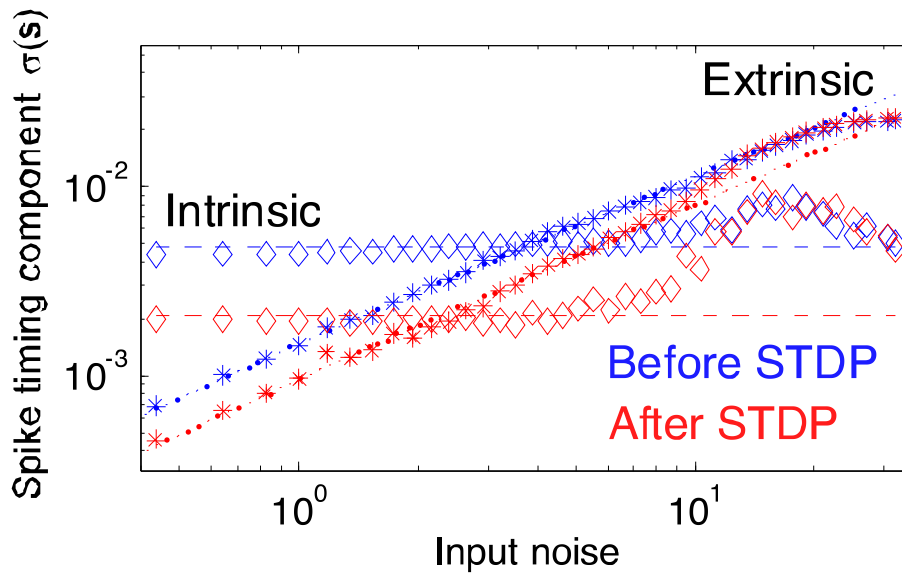
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# Extrinsic noise limits timing improvement



Timing precision (circles) is the sum (bold dots) of intrinsic and extrinsic variability; dashed and dotted lines are linear extrapolations of intrinsic and extrinsic variability; continuous line is their sum.

# STDP reduces both extrinsic and intrinsic variance

STDP reduces the variance of both intrinsic and extrinsic components (*dashed and dotted lines*, linear fits).

STDP works below a noise level of 10 (a.u.). In this regime, it reduces the extrinsic as well as intrinsic components of variance. The former was expected but the latter is surprising.
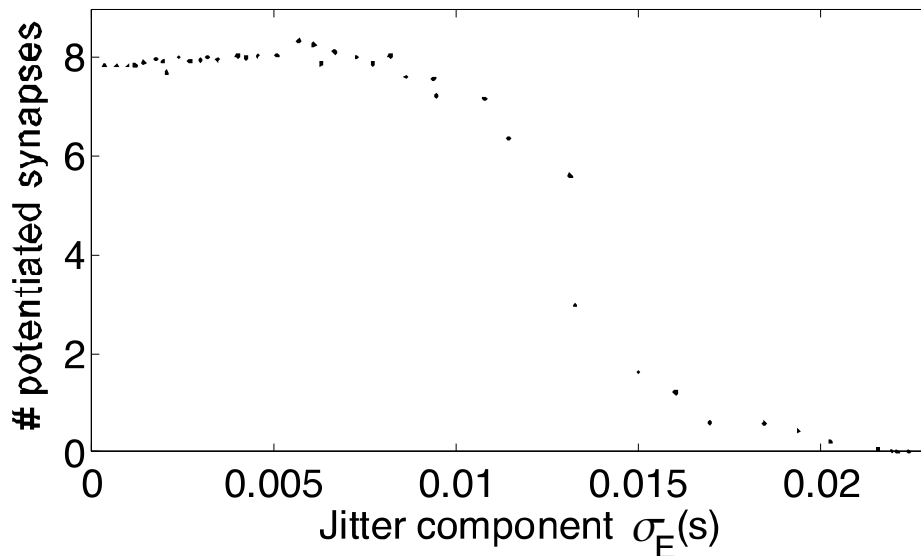
There are two possible explanations:

–Less noisy input from recurrent synapses dominates

–Jitter decreases with latency ($\sigma_n \propto \mu_n$)

The apparent increase in the intrinsic component at high noise levels is an artifact. It is difficult to estimate $\mu_n$ when neuron $n$'s spike are jittering all over the place. These errors in $\mu_n$ increase $\sigma_I = \sigma[\mu_n]$.
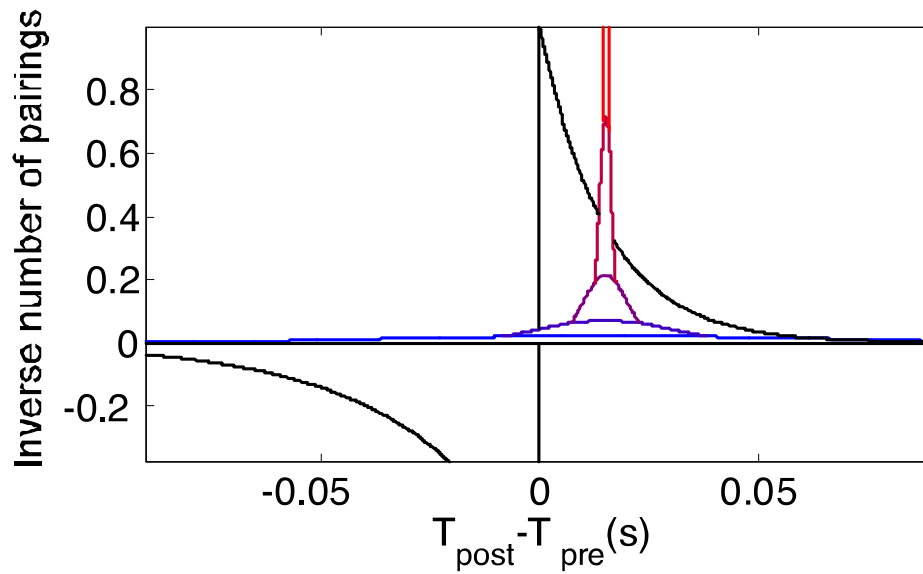
# Extrinsic variability breaks STDP



The average number of potentiated synapses per neuron drops as extrinsic noise increases; each neuron 21 synapses total. Synaspse don't potentiate when $\sigma_E$ exceeds 12ms.

Intrinsic variability gives rise to timing-differences, which drive STDP, while extrinsic variability gives rise to jitter, which frustrates STDP.
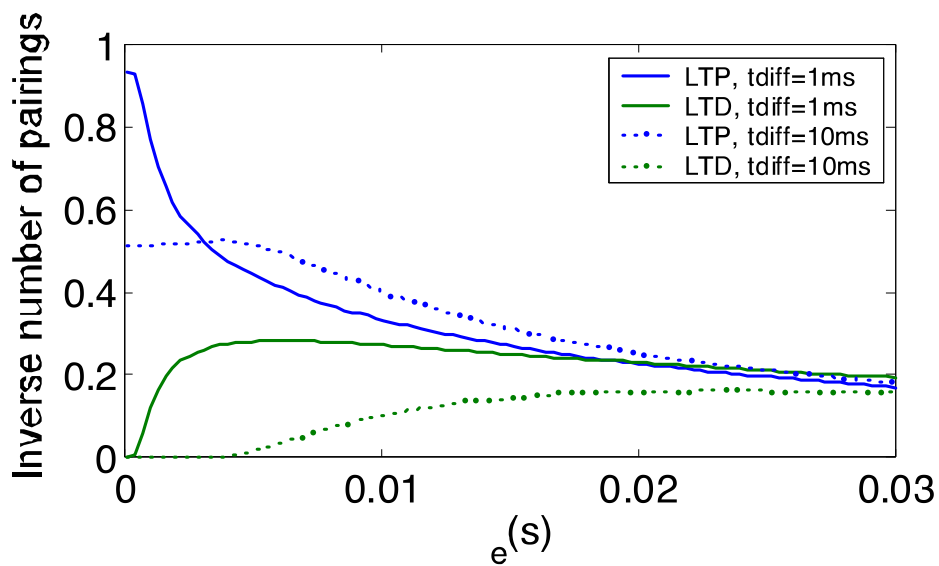
# Pre-post timing distribution broadens



As extrinsic variability increases, the distribution of pre-post time differences spreads (red→blue),  and even changes sign, as post-pre pairings start to occur, canceling the contributions of pre-post pairings.

# Predicting when STDP breaks

Drawing timing differences from a distribution, and adding the right amount to the potentiation and depression integrators, we found the average number of pairings required for them to reach threshold.

With increasing extrinsic variability,

more pairings are required to reach the potentiation threshold and hence efficacy drops when $\sigma_E$

becomes comparable to $t_{pair}$ (labeled $t_{diff}$ in this figure). This drop off occurs becauses pairings stop contributing

when their sign flips (become post − pre) and when their time

− difference becomes too long (tails of distribtution). The former contribute to the depression integrator,

hence the synapses depresses when initiated to the potentiated state.

# Next week: Associative memory
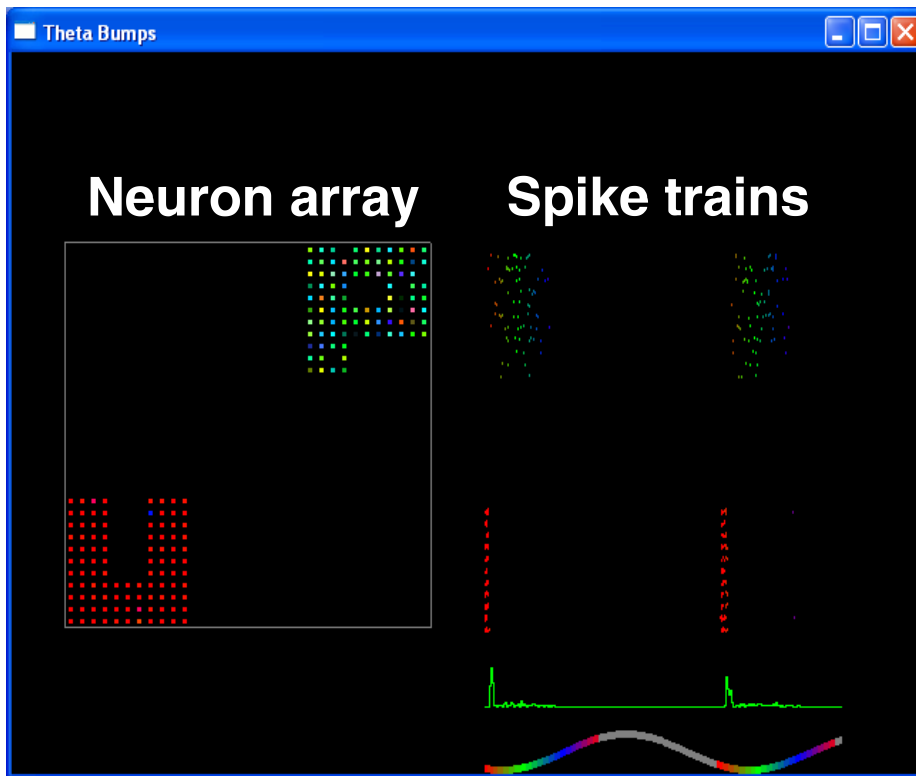


Memories are stored by potentiating synapses among coactivated neurons.